
PHYLOGENETIC INFLUENCE ON TWINING CHIRALITY IN LIANAS FROM AMAZONIAN PERU¹

Robyn J. Burnham² and Caissa Revilla-Minaya³

ABSTRACT

A majority of angiosperm species of vines and lianas use their stem apices for twining and adherence to support structures. Prior observations have suggested a strong predominance of twining orientation in a dextral (right-handed) direction. We present here the chirality of twining (handedness) for 60 taxa representing 21 families encountered in a terra firme Amazonian forest community in Peru. We surveyed 145 stems of climbers that represented one to eight individuals of a given taxon. We demonstrate that dextral chirality is phylogenetically widespread among angiosperm stem climbers and suggest that phylogenetic deviations from the dextral pattern represent independent evolutionary events. Phylogenetic constraint might be invoked to explain the dextral dominance among climbers, but dextral circumnutation is not ubiquitous in other angiosperm organs. Here we also clearly define climbing chirality because of the confusion in previous literature, and we compile published family-level reports of deviations from dextral orientation. This study underscores the need for approaching the twining chirality of plants from genetic, developmental, and physiologic perspectives to clarify the basis for the preferred twining orientation among angiosperm climbers.

RESUMEN

La mayoría de las especies de lianas y enredaderas angiospermas utilizan los ápices de sus tallos para enredar y adherirse a las estructuras que les sirven de soporte. Observaciones empíricas muestran una marcada preferencia por una dirección de enrollamiento dextral (hacia la derecha). Presentamos a continuación la dirección de quiralidad preferida por 60 especies de 21 familias de plantas trepadoras encontradas en un bosque Amazónico de tierra firme en Perú. Evaluamos 145 tallos de trepadoras que representaron entre uno y ocho individuos de cada morfotipo. Nos demostramos que la quiralidad dextral está ampliamente distribuida filogenéticamente entre las angiospermas trepadoras y sugerimos que desviaciones filogenéticas del patrón dextral representan eventos evolutivamente independientes. Las restricciones filogenéticas pueden explicar la dominancia dextral entre trepadoras, pero el quiralidad dextral aparentemente no es omnipresente entre otros órganos de angiospermas. En este estudio también definimos claramente la quiralidad de trepar debido a la confusión en previos trabajos, y recopilamos reportes publicados a nivel de familias sobre desviaciones de la quiralidad dextral. Este estudio resalta la necesidad de enfocar la dirección de enrollamiento de las plantas desde las perspectivas genética, del desarrollo, y fisiológica para aclarar el origen de la preferencia de dirección de enrollamiento en las angiospermas trepadoras.

Key words: Amazonia, chirality, dextral, handedness, liana, Los Amigos, Peru, sinistral, twiner, vine.

Climbing plants (vines and lianas) ascend using the structural support of a host plant or structure. Mechanisms and organs used for attaching to and climbing a host include twining stem apices, tendrils (axillary, petiolar, or leaf), spines, adventitious roots, stem-derived hooks, and simple scrambling. Although the mechanism employed for ascent can vary, within most families only one mechanism is normally found. For example, almost all climbing species of Bignoniaceae ascend using tendrils modified from the terminal leaflet of a trifoliate leaf; almost all species of Apocynaceae climb by twining stems; the climbing Celastraceae generally use either touch-sensitive

axillary branches (Hippocrateoideae and Salicoideae) or stem twining (Celastraceae); and most Cucurbitaceae and Passifloraceae climb using axillary determinate stems modified as coiling tendrils. One exception is the large legume family, Fabaceae, in which almost all types of climbing mechanisms can be found.

Table 1 summarizes the primary climbing mechanism of Neotropical climbers from 49 families based on our observations from field sites in Amazonia and literature reviews (see Table 1 for sources). Few families exhibit more than one strategy for climbing, suggesting that climbing mechanism is strongly correlated with phylogeny (Hegarty, 1991; Ornduff,

¹ The authors gratefully acknowledge a grant to R.J.B. from the Amazon Conservation Association to fund research at the Los Amigos Biological Station. John P. Langmore, Nigel C. A. Pitman, Elizabeth Palazzola, Wendy K. Silk, Ricardo Cardosa Vieira, and an anonymous reviewer gave constructive comments on early versions of the manuscript. Bonnie Miljour rendered the fine sketch of circumnutating vines.

² Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109-1079, U.S.A. Author for correspondence: rburnham@umich.edu.

³ Department of Anthropology, Vanderbilt University, VU Station B, Box 6050, Nashville, Tennessee 37235, U.S.A. caissarevillaminaya@yahoo.com.

doi: 10.3417/2008080

2004; Jongkind, 2005). The largest number of climber families ascend by means of circumnutating apices (hereafter termed “twiners”), which appears to be a recurrent evolutionary innovation that has arisen repeatedly in angiosperms, as noted by Darwin (1876).

Normally twiners do not produce tendrils of any sort, thus achieving their upward movement by strong apical helices (axial tension) and frictional force (normal distributed load) on the support structure (Bell, 1958; Silk & Hubbard, 1991; Scher et al., 2001; Silk & Holbrook, 2005). Although the circumnutating stem has its movement arrested at the point of contact with the support, its free apical portion continues circumnutating in the same direction and thus continues upward, wrapping around the support. Interestingly, it has been mentioned by several authors that almost all twiners circumnutate in the same direction (dextrally), and almost all individuals of a species in the same direction (Sachs, 1882; Cribb, 1985; Ornduff, 1991; Hashimoto, 2002; Ford & Purrington, 2004; Lubkin, 2004). Etien and Traoré (2005) reported that 85% of the liana stems encountered in an African forest were dextrally twining, although their data on twining orientation were not published at the species level.

The physiological or anatomical basis for this consistent twining chirality has not been determined, to our knowledge, but has attracted attention from systematists, physicists, physiologists, and mathematicians. Circumnutation itself is caused by a wave of cell elongation on one side of the young internode, and this wave migrates around the stem, causing the bending on the opposite side (Darwin, 1876; Darwin & Darwin, 1881). At the physiological level, the bending is caused by water imbalance on one side of the stem where it causes cells to increase their turgidity and elongate (Lubkin, 2004). To explain circumnutation, different authors have suggested roles for phototropism (Sachs, 1882), thigmotropism (Darwin & Darwin, 1881), geotropism/gravitropism (Israelsson & Johnsson, 1967; Kitazawa et al., 2005), microfibril orientation in xylem (Silk & Hubbard, 1991; Ford & Purrington, 2004), microtubule orientation in cells (Thitamadee et al., 2002; Edwards et al., 2007), epidermal cell anisotropism (Hashimoto, 2002), and anatomical asymmetry (Silk & Hubbard, 1991; Lubkin, 2004; Bowling & Vaughn, 2009). Whatever the ultimate cause, it is clear that once a circumnutating vine begins to twine in a specific orientation, it almost always continues that trajectory, maintaining friction and external pressure against its support, which allows for its ascent (Putz & Holbrook, 1991; Silk & Holbrook, 2005). A

complete biological explanation for the mechanism of apical twining must also involve the widespread predominance of dextral twining orientation. Chirality has been observed in a variety of other plant organs (hypocotyls, coleoptiles, roots, petioles, petals, wood), but a predominant chirality across all organs (Hashimoto, 2002; Säll, 2002; Kitazawa, 2005; Mugnal, 2007) has not been observed, to our knowledge.

During fieldwork in Amazonian Ecuador and from casual observations in Peru, Brazil, Bolivia, and the eastern United States, the first author observed that most species of twiners circumnutate dextrally. This led to observations in a variety of field sites, in which it was observed that latitude did not influence the predominance of dextral circumnutation (see also Ornduff, 2004; Edwards et al., 2007).

Here we define circumnutation in three congruent ways to facilitate comparisons with data that exist in the literature (Fig. 1; Table 2). Dextral circumnutation is defined as circumnutation from left to right when observing the upward route of the vine on the support, and conversely sinistral circumnutation is a route from right to left. These terms are equivalent to clockwise and counterclockwise, respectively, when observing the vine from the base of the stem upward, which takes into account the frame of reference taken by the apex of the plant. Darwin's (1876) observations on climbing orientation in vines were recorded as those that move against the sun versus those that follow the sun (dextral and sinistral, respectively). So, counterclockwise (CCW) is equivalent to right to left and to follows the sun. Twining chirality is also referred to in the literature as handedness, with dextral being right handed and sinistral left handed (Kihara, 1972; Ornduff, 1991, 2004; Ford & Purrington, 2004). The simple use of clockwise and CCW (or anticlockwise) is misleading, as this can be differently interpreted whether the climber is viewed from the base of the stem upward, or from the apex downward. Thus, the perspective of observation should always be included where these terms are used (see Allard, 1947; Ornduff, 1991, 2004; Larson, 2000; Edwards et al., 2007 for reports on handedness in which they took the point of reference as from above the stem, and thus their CCW should be clockwise by the system detailed here). We strongly recommend the use of the right-handed and left-handed terms (or dextral/sinistral). As a final note, a convention that never seems to have gained acceptance is the encyclopedic work of Baillaud (1962: 660), who invoked the terms positive and negative for what we designate here as dextral and sinistral, respectively. Kihara (1972) presented a

Table 1. Primary climbing mechanism found in species of 49 families of tropical plants. All mechanisms are based on field observations from Costa Rica, Ecuador, Peru, and Brazil (noted as RJB, pers. obs., only in cases of sole source), in addition to literature sources as cited below. Most families include only one type of climbing mechanism.

Family	Stem twining	Axillary tendrils: stem/inflorescence modification	Tendrils: modified leaf and petiole	Spines/tendrils: modified stipules	Root climbing	Thorny/spiny stems and scramblers	Literature source
Acanthaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Apocynaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004; Livshultz et al., 2007
Aristolochiaceae	X						Darwin, 1876; Sachs, 1882; Baillaud, 1962; Ornduff, 2004
Asteraceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Basellaceae	X						Ornduff, 2004
Boraginaceae	X						Baillaud, 1962; DeWalt et al., 2000; Ornduff, 2004
Caprifoliaceae	X						Darwin, 1876; Larson, 2000; Ornduff, 2004
Celastraceae	X	X					Croat, 1978; Ornduff, 2004; RJB, pers. obs.
Combretaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Connaraceae	X	X					Acevedo-Rodríguez, 2005; RJB, pers. obs.
Convolvulaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Dichapetalaceae	X	X					Hegarty & Caballé, 1991; Jongkind, 2005
Dilleniaceae	X						Darwin, 1876; Baillaud, 1962; Ornduff, 2004
Dioscoreaceae	X						Baillaud, 1962; Hegarty & Caballé, 1991; Ornduff, 2004
Euphorbiaceae	X						Baillaud, 1962; Putz, 1984; Ornduff, 2004
Fabaceae	X	X	X	X		X	Darwin, 1876; Baillaud, 1962; Lewis, 1987; Ornduff, 2004; Acevedo-Rodríguez, 2005
Gnetaceae	X						Carlquist, 1996; Ornduff, 2004
Icacinaceae	X						Ornduff, 2004
Lamiaceae	X						Darwin, 1876; Ornduff, 2004
Malpighiaceae	X						Baillaud, 1962; Hegarty & Caballé, 1991; Ornduff, 2004
Menispermaceae	X						Baillaud, 1962; Hegarty & Caballé, 1991; Ornduff, 2004
Olacaceae	X						RJB, pers. obs.
Piperaceae	X				X		Hegarty & Caballé, 1991; Pinard & Putz, 1994; RJB, pers. obs.

Table 1. Continued.

Family	Stem twining	Axillary tendrils: stem/inflorescence modification	Tendrils: modified leaf and petiole	Spines/tendrils: modified stipules	Root climbing	Thorny/spiny stems and scramblers	Literature source
Polygonaceae	X	X					Sachs, 1882; Baillaud, 1962; Putz, 1984; DeWalt et al., 2000; Ornduff, 2004
Rubiaceae	X			X		X	Darwin, 1876; Hegarty & Caballé, 1991; Putz & Holbrook, 1991; Ornduff, 2004
Verbenaceae	X						Baillaud, 1962; Putz, 1984; Ornduff, 2004
Violaceae	X						Baillaud, 1962; RJB, pers. obs.
Annonaceae		X					Johnson, 2003
Cucurbitaceae		X					Gerrath et al., 2008
Hernandiaceae			X				Ribeiro et al., 1999
Loganiaceae		X					Putz & Holbrook, 1991
Passifloraceae		X					Hegarty & Caballé, 1991
Polygalaceae		X		X			Acevedo-Rodríguez, 2005; RJB, pers. obs.
Rhamnaceae		X					Acevedo-Rodríguez, 2005
Sapindaceae		X					Acevedo-Rodríguez, 2005
Ulmaceae		X					Acevedo-Rodríguez, 2005
Vitaceae		X			X		Hegarty & Caballé, 1991; DeWalt et al., 2000; RJB, pers. obs.
Arecaceae			X				Croat, 1978; Hegarty & Caballé, 1991
Bignoniaceae			X				Hegarty & Caballé, 1991
Ranunculaceae			X				Acevedo-Rodríguez, 2005
Smilacaceae				X			Pinard & Putz, 1994; Acevedo-Rodríguez, 2005
Anacardiaceae					X		RJB, pers. obs.
Araceae					X		Hegarty & Caballé, 1991
Araliaceae					X		Metcalfé, 2005
Begoniaceae					X		Sands, 2009
Hydrangeaceae					X		Nevling, 1964
Melastomataceae					X		Schulman & Hyvönen, 2003
Schlegeliaceae					X		Acevedo-Rodríguez, 2005
Malvaceae						X	Croat, 1978

thorough review of botanical perspectives on handedness terminology up to the early 1970s.

We present here an exhaustive survey of a local climber flora in which handedness of apically twining species is recorded. In contrast to the globally oriented work of Edwards et al. (2007) in which they traversed a trail, counting the first 17 to 121 climbing stems (average of 81) at each of 17 sites (one of which was the Los Amigos site addressed here), we studied a geographically limited climber flora, including as many distinct taxa as possible. This difference between the two studies corrects for the probability

of including large numbers of individuals of the same taxon when only the first-encountered, unidentified stems are evaluated, thus decreasing the phylogenetic breadth of the census. Our study addresses climbing plants exclusively from the Neotropics, and thus is also a departure from the excellent compendium of Ornduff (2004) in which plants observed were largely under cultivation in botanical gardens and in which the species observed were predominantly from Africa, Asia, and Australia.

Using our survey, we tested the hypothesis that distinct taxa within a flora are expected to twine

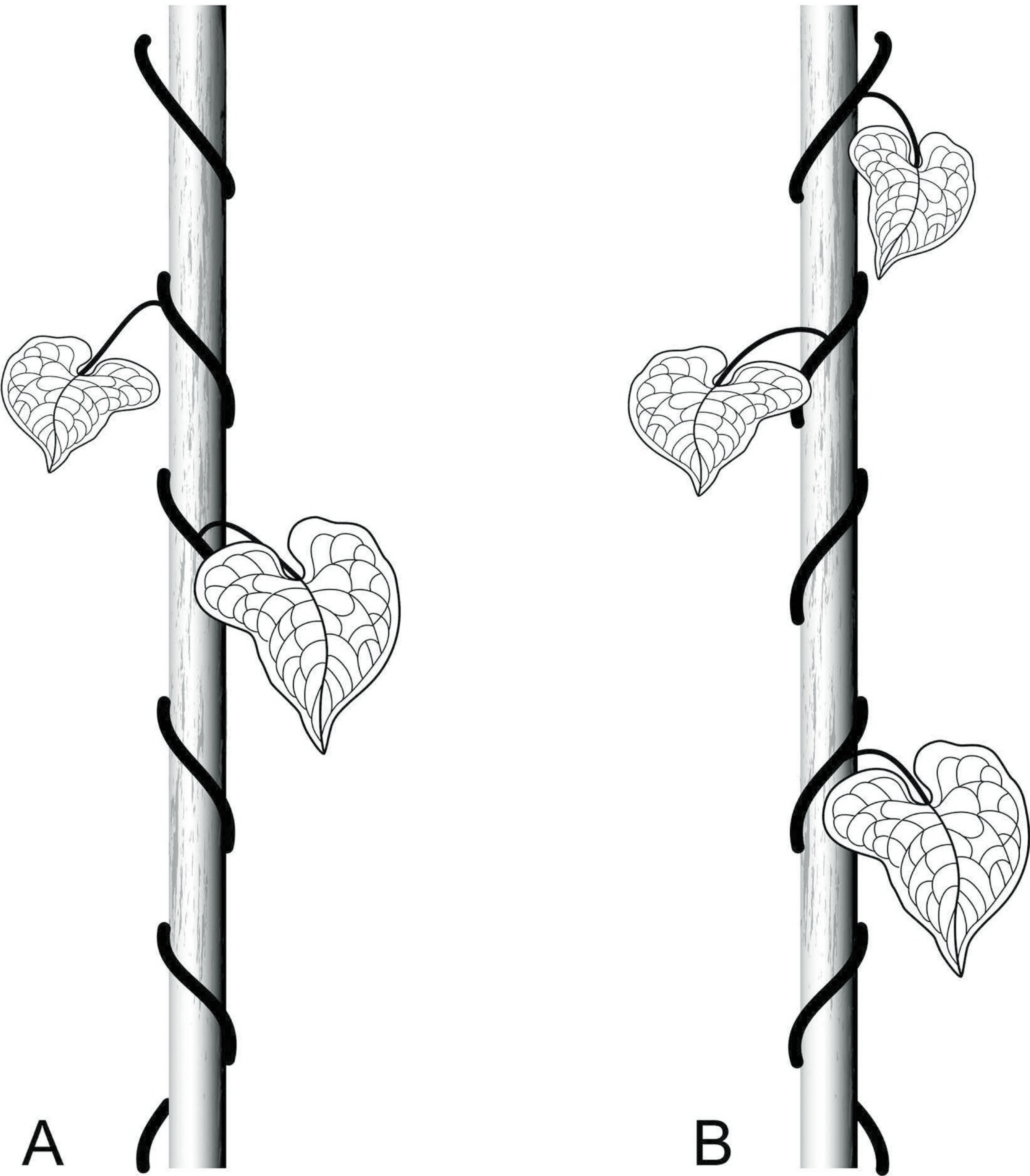


Figure 1. Twining orientation used in this paper. —A. Stem is a sinistral climber, twining from right to left. —B. Stem is a dextral climber, twining from left to right.

Table 2. Explicit definitions and equivalence of twining chirality used in this paper, with notes aiding comparison to other studies.

		Notes
Dextral	Sinistral	Least equivocal terminology.
Right handed	Left handed	Synonyms for dextral and sinistral.
Clockwise	Counterclockwise	If used, this must specify observation perspective as from base of plant; if viewed from above these terms will be reversed; our observation points were from the base of the plant.
Positive	Negative	Designation by Baillaud (1962), whose justification for a new term was that the historical origin of dextral and sinistral was confusing.
Moves against the sun	Follows the sun	Darwin (1876); note this is correct only for Northern Hemisphere observations.

predominantly with a dextral chirality (rather than 50% dextral, 50% sinistral). Further, we evaluated the earlier observations that twining chirality (and thus circumnutation) is phylogenetically constrained among angiosperm families that include climbers. Here we propose that if individual censuses (that is, counting every stem in an area) differ from taxa-based censuses in twining chirality patterns, it may suggest that there is an ecological advantage to sinistral twining, despite the predominance of dextral orientation among species. For example, if sinistrally climbing individuals are present in higher proportions than sinistrally climbing taxa, it would suggest that sinistral orientation may be linked to ecological success.

METHODS

Our work was carried out in southeastern Peru (Madre de Dios Region) at the Los Amigos Biological Station (12°34'07"S, 70°05'57"W). During a complete census of two 0.5-ha forest plots for climber distribution, diversity, and density, we also made observations on the orientation of climbing in stem-twining species. We also surveyed the margins of 5.2 km of forested trails in the area to record twining chirality. We included up to eight individuals of the same taxon in our tallies. We chose eight as a maximum observation number, based on the probability (1 in 250) of incorrectly coding a taxon as demonstrating a single twining chirality if both dextral and sinistral were present in equal numbers in the population. In reality, most climbing taxa are sufficiently rare in the Los Amigos area, so that we observed most taxa only two to three times. Thus, we maximized phylogenetic diversity and minimized duplicate observations of the same taxon. We excluded from our observations all taxa whose main mechanism of ascent is by tendrils, hooks, or spines (e.g., members of the Sapindaceae, Bignoniaceae, Passifloraceae, Rhamnaceae, etc.), even if their stems weakly twined. We arbitrarily chose to record an individual only when the stem twined at least three times around its support. In evaluating stems for the census, we excluded any individual of a taxon seen within 20 m of the last observation of that same taxon to avoid, as much as possible, censusing the same individual (via cloning) more than once. All individuals were growing in densely shaded terra firme habitats, and all were vigorously growing adults but without evident fruits or flowers, i.e., currently sterile specimens.

Individuals censused were included if we could identify the taxon at least to family. Morphospecies

names were used to designate distinct entities for unknown species or genera. Observations were combined into single morphospecies for cases in which we were not confident of the distinctness of the individuals in question. Thus, we estimate that there is more taxonomic diversity represented than we report. Herbarium vouchers were made of species from the 0.5-ha plots, but not from all individuals from trail censuses (see Table 3). Specimens are deposited at Universidad Agraria La Molina in Lima, Peru (MOL), and at the University of Michigan Herbarium (MICH), U.S.A. Based on the first author's experience with climbers of the western Amazon region, we are confident of our placement of the individuals counted into the proper taxonomic group.

RESULTS AND DISCUSSION

A total of 145 climbing individuals were recorded for chirality (dextral vs. sinistral), representing 60 distinct taxa (Table 3). We identified 27 individuals only to family, 37 individuals to genus, and 81 to species. The 60 taxa represent 21 families in which the dominant mode of climbing is by stem twining. In 17 of the 21 families, twining chirality was dextral, whereas three families were consistently sinistral and one family included individuals whose stems switched back and forth between sinistral and dextral. At the species level, the pattern is equally clear, with 50 of 60 (83%) taxa circumnating dextrally. This is congruent with, although lower than, a global average of 92.4% dextral orientation in unidentified stems surveyed by Edwards et al. (2007: 795). Their Los Amigos average was 86.8% based on the site count of 79 unidentified stems.

Our census included a large proportion of the climbing taxa in the area of Los Amigos. In our censuses of two 0.5-ha plots, we encountered ca. 70 and 80 species of lianas in the two plots (stems ≥ 1 cm diam.; unpubl. data). Of those species, about 35 and 40 species, respectively, were stem twiners, while the remainder was a mix of tendrillate, hooking, root-climbing, spiny, and scrambling lianas. Thus, we believe that our observations of 60 taxa from Los Amigos trails, combined with observations made on the two 0.5-ha plots, include most of the stem-twining taxa in the area of the Los Amigos Biological Station. The data are thus a taxon-based (vs. stem-based) census of the twining chirality of climbers at Los Amigos.

Taxa that only circumnated sinistrally included all specimens of the Dioscoreaceae, Piperaceae, and Asteraceae, and only taxa in these families (Table 3). Although our survey included only one or two species

Table 3. Summary of chirality in 60 twining taxa observed at the Los Amigos Biological Station, Peru. No individuals were censused within 20 m of another individual of the same taxon to avoid censusing clonal individuals. One to eight individuals were censused per taxon; total number of individuals censused was 145.

Family	Genus	Species or morphospecies	Burnham collection number ¹	No. of individuals observed	Twining chirality ²
Acanthaceae	<i>Mendoncia</i> Vell. ex Vand.	sp. indet. 1	RJB 3433	3	D
Acanthaceae	<i>Mendoncia</i>	<i>sericea</i> Leonard	RJB 3669	3	D
Acanthaceae	<i>Mendoncia</i>	sp. indet. 3	RJB 3713, RJB 3596	3	D
Apocynaceae	<i>Forsteronia</i> G. Mey.	<i>amblybasis</i> S. F. Blake	RJB 3611	7	D
Apocynaceae	<i>Forsteronia</i>	<i>acouci</i> (Aubl.) A. DC.	RJB 3568, 3661	2	D
Apocynaceae	<i>Odontadenia</i> Benth.	<i>puncticulosa</i> (Rich.) Pulle	RJB 3491	1	D
Apocynaceae	<i>Odontadenia</i>	<i>verrucosa</i> (Willd. ex Roem. & Schult.) K. Schum. ex Markgr.	RJB 3584	1	D
Apocynaceae	<i>Gonolobus</i> Michx.	sp. indet. 1	RJB 3557	3	D
Apocynaceae	genus indet. 1	sp. indet. 1	—	2	D
Apocynaceae	genus indet. 2	sp. indet. 1	—	1	D
Aristolochiaceae	<i>Aristolochia</i> L.	sp. indet. 1	—	1	D
Aristolochiaceae	<i>Aristolochia</i>	sp. indet. 2	—	1	D
Aristolochiaceae	<i>Aristolochia</i>	<i>dalyi</i> F. González	RJB 3690, 3712	2	D
Asteraceae	<i>Mikania</i> Willd.	<i>guaco</i> Humb. & Bonpl.	RJB 3499	8	S
Asteraceae	<i>Mikania</i>	sp. indet. 1	—	1	S
Combretaceae	<i>Combretum</i> Loefl.	<i>laxum</i> Jacq.	RJB 3542, 3616	7	D
Combretaceae	<i>Combretum</i>	<i>assimile</i> Eichler	RJB 3664	1	D
Combretaceae	genus indet. 1	sp. indet. 1	RJB 3587	1	D
Connaraceae	<i>Pseudoconnarus</i> Radlk.	<i>macrophyllus</i> (Poepp.) Radlk.	RJB 3561	1	D
Convolvulaceae	<i>Ipomoea</i> L.	sp. indet. 1	—	5	D
Convolvulaceae	<i>Maripa</i> Aubl.	sp. indet. 1	RJB 3670	1	D
Convolvulaceae	<i>Dicranostyles</i> Benth.	sp. indet. 1	RJB 3586	1	D
Dichapetalaceae	<i>Dichapetalum</i> Thouars	sp. indet. 1	RJB 3738	2	D
Dilleniaceae	genus unknown	sp. indet. 1	RJB 3490, 3551	2	S, D
Dilleniaceae	genus unknown	sp. indet. 2	RJB 3488	4	S, D
Dilleniaceae	genus unknown	sp. indet. 3	RJB 3583	4	S, D
Dilleniaceae	genus unknown	sp. indet. 4	RJB 3520	2	S, D
Dilleniaceae	genus unknown	sp. indet. 5	RJB 3688	2	S, D
Dioscoreaceae	<i>Dioscorea</i> L.	sp. indet. 1	—	2	S
Euphorbiaceae	<i>Plukenetia</i> L.	<i>brachybotrya</i> Müll. Arg.	RJB 3684	2	D
Fabaceae	<i>Deguelia</i> Aubl.	sp. indet. 1	RJB 3654	3	D
Fabaceae	genus unknown	sp. indet. 1	—	3	D
Fabaceae	genus unknown	sp. indet. 2	RJB 3639	1	D
Fabaceae	genus unknown	sp. indet. 3	—	1	D
Hernandiaceae	<i>Sparattanthelium</i> Mart.	<i>tarapotanum</i> Meisn.	RJB 3706, 3721	1	D
Malpighiaceae	<i>Mezia</i> Schwacke ex Nied.	sp. indet. 1	RJB 3426	4	D
Malpighiaceae	genus unknown	sp. indet. 2	—	3	D
Malpighiaceae	genus unknown	sp. indet. 3	—	1	D
Malpighiaceae	<i>Banisteriopsis</i> C. B. Rob.	<i>muricata</i> (Cav.) Cuatrec.	RJB 3437	1	D
Malpighiaceae	<i>Mascagnia</i> (Bertero ex DC.) Colla	<i>dissimilis</i> C. V. Morton & Moldenke	RJB 3521	2	D
Malpighiaceae	<i>Hiraea</i> Jacq.	<i>fagifolia</i> (DC.) A. Juss.	RJB 3702	4	D
Malpighiaceae	<i>Hiraea</i>	sp. indet. 2	—	1	D
Malpighiaceae	<i>Tetrapteryx</i> Cav.	sp. indet. 1	RJB 3566	1	D
Malvaceae	<i>Byttneria</i> Loefl.	<i>benensis</i> Britton	RJB 3715	2	D
Menispermaceae	<i>Sciadotenia</i> Miers	<i>toxifera</i> Krukoff & A. C. Sm.	RJB 3710, 3567	2	D
Menispermaceae	<i>Abuta</i> Aubl.	<i>rufescens</i> Aubl.	—	2	D
Menispermaceae	<i>Anomospermum</i> Miers	<i>grandifolium</i> Eichler	—	4	D
Menispermaceae	<i>Anomospermum</i>	<i>chloranthum</i> Diels	RJB 3692	4	D

Table 3. Continued.

Family	Genus	Species or morphospecies	Burnham collection number ¹	No. of individuals observed	Twining chirality ²
Menispermaceae	<i>Cissampelos</i> L.	<i>pareira</i> L.	RJB 3478	2	D
Menispermaceae	<i>Disciphania</i> Eichler	sp. indet. 1	RJB 3461	3	D
Menispermaceae	<i>Telitoxicum</i> Moldenke	<i>minutiflorum</i> (Diels) Moldenke	RJB 3735	1	D
Olacaceae	<i>Heisteria</i> Jacq.	<i>scandens</i> Ducke	RJB 3647	2	D
Piperaceae	<i>Manekia</i> Trel.	<i>sydowii</i> (Trel.) T. Arias, Callejas & Bornst.	RJB 3568	3	S
Piperaceae	<i>Piper</i> L.	sp. indet. 1	—	2	S
Polygonaceae	<i>Coccoloba</i> P. Browne	<i>excelsa</i> Benth.	RJB 3425	3	D
Polygonaceae	<i>Coccoloba</i>	<i>marginata</i> Benth.	RJB 3435	5	D
Polygonaceae	<i>Coccoloba</i>	<i>parimensis</i> Benth.	RJB 3588	2	D
Rubiaceae	<i>Manettia</i> Mutis ex L.	<i>cordifolia</i> Mart.	—	1	D
Verbenaceae	<i>Petrea</i> L.	<i>blanchetiana</i> Schauer	RJB 3585	1	D
Verbenaceae	<i>Petrea</i>	<i>maynensis</i> Huber	RJB 3608	4	D

¹ Collection numbers provided only for collected specimens; vouchered specimens are deposited at MOL and MICH.
² D = dextral, S = sinistral.

in each of these families (16 of the 145 individuals, 11%), our results on the frequency of sinistral circumnutation are supported by our observations from other regions of the Amazon Basin as well as in the temperate zone of North America (R. J. Burnham, unpubl. data). Literature documentation (Darwin, 1876; Baillaud, 1962; Ornduff, 2004) of temperate and tropical genera exhibiting sinistral twining also includes *Humulus* L. spp. (Cannabaceae); *Fallopia* Adans., *Muehlenbeckia* Meisn., and *Polygonum* L. spp. (Polygonaceae); *Scyphanthus elegans* Sweet (Loasaceae); various members of the Rubiaceae; all members of the Illiciaceae that have been observed; and *Clerodendrum* L. spp. (Lamiaceae). Possibly closely related to *Clerodendrum* are members of *Petrea* L. (Verbenaceae), which was observed to twine dextrally at Los Amigos.

The Dilleniaceae deserves special mention because of its curious behavior. In almost all individuals and taxa observed, stems circumnutated in one direction, and after two to three revolutions they changed direction and circumnutated in the opposite direction for two to three revolutions. We observed two sequential changes in twining direction in at least 10 of the 14 individuals of Dilleniaceae that we included in our observations. Darwin also noted this curious behavior in a single dilleniaceous individual of *Hibbertia* Andrews (Darwin, 1876: 26, 36). Darwin also observed that the Loasaceae species *Loasa aurantiaca* Urb. & Gilg and *Scyphanthus elegans* exhibit chirality changes in individual stems. Here we call this phenomenon ambidextrous twining when encountered within a single species. The largely temperate species *Solanum dulcamara* L. is

another example of ambidextrous twining (Dufour, 1902; Baillaud, 1962; Ornduff, 2004), but it also employs the scrambling mechanism, which assists in supporting the individuals as they climb. These are the only species we are aware of with a change in chirality during ontogeny. We have only observed this occurring in members of the Dilleniaceae, and have never seen any of the dextrally circumnutating species showing evidence of reversing direction during growth.

Chirality of twiners is phylogenetically correlated, with almost every family that includes stem-twinning taxa showing consistently dextral circumnutation, and those that are sinistral also showing consistency within the family. Our census included eight families represented by a single taxon (12 individuals) and 13 families represented by two to seven taxa. Within each family, the taxa show consistent chirality. This suggests that climbing orientation may be nearly universal within a family. The interesting deviations from the typically dextral chirality of species at Los Amigos are not phylogenetically closely related. Piperaceae is a member of the Magnoliid basal angiosperm clade, Dioscoreaceae is a monocot, and Asteraceae is a member of the euasterid campanuliid clade (Angiosperm Phylogeny Group III, 2009). Dilleniaceae (the family in which inconsistent orientation was noted) has been placed as a sister to Caryophyllales and is a basal core eudicot, again not particularly close to any of the other sinistral families. There are some intriguing reports of families in which both dextral and sinistral chirality can be found: Baillaud (1962) reported *Anchietea* A. St.-Hil. as dextral and *Corynostylis* Mart. & Zucc. as sinistral,

both of which are woody climbing members of the Violaceae. The same author reported species of *Dioscorea* L. twining dextrally or sinistrally, or able to change direction during ontogeny. These reports are exciting, although they stem from relatively few observations. Still, these exceptions may provide a fertile avenue for investigating the basis for chiral asymmetry among flowering plants.

Our data represent a phylogenetically broad and floristically complete perspective on previous observations on the predominance of twining chirality. It documents the phylogenetic distribution of chirality among twiners in a single Amazonian forest and underscores the gap in our understanding of the predominance of dextral orientation among angiosperm twiners. The stem-twining habit has clearly evolved multiple times in different angiosperm lineages, as evidenced by the mix of ancestral habits (shrub, tree, climber) found among angiosperm clades (Angiosperm Phylogeny Group III, 2009). A developmentally based argument for the importance of dextral chirality in climbers must also include a perspective on the chirality in organs of nonclimbers (e.g., flowers, buds, wood) that would be consistent with such an explanation. The literature indicates no similar chirality predominance in other plant organs (Gardner, 1990; Endress, 2001; Welch, 2002). Why the orientation of stem-twiners should be so consistently dextral has not yet been adequately answered by recent research on the physical properties of circumnutation and support of vines (Silk & Hubbard, 1991; Silk & Holbrook, 2005; Goriely & Neukirch, 2006; Bowling & Vaughn, 2009).

Literature Cited

- Acevedo-Rodríguez, P. 2005. Vines and climbing plants of Puerto Rico and the Virgin Islands. *Smithsonian Contr. Bot.* 51: 1–483.
- Allard, H. A. 1947. The direction of twist of the corolla in the bud, and twining of the stems in Convolvulaceae and Dioscoreaceae. *Castanea* 12(3): 88–94.
- Angiosperm Phylogeny Group III. 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Bot. J. Linn. Soc.* 161(2): 105–121.
- Baillaud, L. 1962. Les mouvements d'exploration et d'enroulement des plantes volubiles. *Handb. Pflanzenphysiol.* 17: 635–715.
- Bell, P. R. 1958. Twining of the hop. *Nature* 181: 1009–1010.
- Bowling, A. J. & K. C. Vaughn. 2009. Gelatinous fibers are widespread in coiling tendrils and twining vines. *Amer. J. Bot.* 96(4): 719–727.
- Carlquist, S. 1996. Wood, bark, and stem anatomy of Gnetales: A summary. *Int. J. Pl. Sci.* 157(6): S58–S76.
- Cribb, A. B. 1985. The direction of twining in some Queensland plants. *Queensland Naturalist* 25: 122–124.
- Croat, T. B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Stanford, California.
- Darwin, C. 1876. *The Movements and Habits of Climbing Plants*, 2nd ed., revised. D. Appleton and Company, New York.
- Darwin, C. & F. Darwin. 1881. *The Power of Movement in Plants*. John Murray, London.
- DeWalt, S. J., S. A. Schnitzer & J. S. Denslow. 2000. Density and diversity of lianas along a chronosequence in a central Panamanian lowland forest. *J. Trop. Ecol.* 16: 1–19.
- Dufour, A. 1902. Climbing plants of Ohio. *Ohio Naturalist* 2: 197–200.
- Edwards, W., A. T. Moles & P. Franks. 2007. The global trend in plant twining direction. *Global Ecol. Biogeogr.* 16: 795–800.
- Endress, P. K. 2001. Evolution of floral symmetry. *Curr. Opinion Pl. Biol.* 4: 86–91.
- Etien, D. T. & D. Traoré. 2005. Climbing plants of the Haut-Sassandra forest: Species and biomorphology. Pp. 137–145 in F. Bongers, M. P. E. Parren & D. Traoré (editors), *Forest Climbing Plants of West Africa: Diversity, Ecology and Management*. CABI Publishing, Cambridge, Massachusetts.
- Ford, E. & C. Purrington. 2004. Determinants of handedness in twining plants. *Sigma Xi Abstract* <<http://www.swarthmore.edu/NatSci/SigmaXi/docs/PosterSummaries2003/ford-emily.pdf>>, accessed 10 February 2011.
- Gardner, M. 1990. *The New Ambidextrous Universe: Symmetry and Asymmetry from Mirror Reflections to Superstrings*. W. H. Freeman and Company, New York.
- Gerrath, J. M., T. B. Guthrie, T. A. Zitnak & U. Posluszny. 2008. Development of the axillary bud complex in *Echinocystis lobata* (Cucurbitaceae): Interpreting the cucurbitaceous tendril. *Amer. J. Bot.* 95: 773–781.
- Goriely, A. & S. Neukirch. 2006. Mechanics of climbing and attachment in twining plants. *Phys. Rev. Lett.* 97: 184301-1–184301-4.
- Hashimoto, T. 2002. Molecular genetic analysis of left–right handedness in plants. *Philos. Trans., Ser. B.* 357: 799–808.
- Hegarty, E. E. 1991. Vine-host interactions. Pp. 357–376 in F. E. Putz & H. A. Mooney (editors), *The Biology of Vines*. Cambridge University Press, Cambridge, United Kingdom.
- Hegarty, E. E. & G. Caballé. 1991. Distribution and abundance of vines in forest communities. Pp. 313–335 in F. E. Putz & H. A. Mooney (editors), *The Biology of Vines*. Cambridge University Press, Cambridge, United Kingdom.
- Israelsson, D. & A. Johnsson. 1967. A theory of circumnutation in *Helianthus annuus*. *Physiol. Pl.* 20: 957–976.
- Johnson, D. M. 2003. Phylogenetic significance of spiral and distichous architecture in the Annonaceae. *Syst. Bot.* 28(3): 503–511.
- Jongkind, J. J. 2005. Checklist of climber species in Upper Guinea. Pp. 231–264 in F. Bongers, M. P. E. Parren & D. Traoré (editors), *Forest Climbing Plants of West Africa: Diversity, Ecology and Management*. CABI Publishing, Cambridge, Massachusetts.
- Kihara, H. 1972. Right- and left-handedness in plants. *Rep. Kihara Inst. Biol. Res.* 23: 1–37.
- Kitazawa, D., Y. Hatakeda, M. Kamada, N. Fujii, Y. Miyazawa, A. Hoshino, S. Iida, H. Fukaki, M. T. Morita, M. Tasaka, H. Suge & H. Takahashi. 2005. Shoot circumnutation and winding movements require grav-

- isensing cells. *Proc. Natl. Acad. Sci. U.S.A.* 102: 18742–18747.
- Larson, K. C. 2000. Circumnutation behavior of an exotic honeysuckle vine and its native congener: Influence on clonal mobility. *Amer. J. Bot.* 87: 533–538.
- Lewis, G. P. 1987. *Legumes of Bahia*. Royal Botanical Gardens, Kew, Richmond.
- Livshultz, T., D. J. Middleton, M. E. Endress & J. K. Williams. 2007. Phylogeny of Apocynoideae and the APSA clade (Apocynaceae s.l.). *Ann. Missouri Bot. Gard.* 94: 324–359.
- Lubkin, S. 2004. Unidirectional waves on rings: Models for chiral preference of circumnutating plants. *Bull. Math. Biol.* 56: 795–810.
- Metcalfe, D. J. 2005. *Hedera helix*. *J. Ecol.* 93: 632–648.
- Mugnai, S. 2007. Nutation in plants. Pp. 72–90 in S. Mancuso & S. Shabala (editors), *Rhythms in Plants: Phenomenology, Mechanisms, and Adaptive Significance*. Springer-Verlag, Berlin.
- Nevling, L. I. 1964. Climbing hydrangeas and their relatives. *Arnoldia (Jamaica Plain)* 24(4–5): 17–39.
- Ornduff, R. 1991. Handedness in twining tracheophytes. *Amer. J. Bot.* 78: 208.
- Ornduff, R. 2004. Handedness in twining tracheophytes. Pp. 1–20 in *Gleanings in Plant Sciences: Festschrift [sic] in Honour of Prof. Bir Bahadur*. Regency Publications, New Delhi.
- Pinard, M. A. & F. E. Putz. 1994. Vine infestation of large remnant trees in logged forest in Sabah, Malaysia: Biomechanical facilitation in vine succession. *J. Trop. Forest Sci.* 6(3): 302–309.
- Putz, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. *Ecology* 65(6): 1713–1724.
- Putz, F. E. & N. M. Holbrook. 1991. Biomechanical studies of vines. Pp. 73–98 in F. E. Putz & H. A. Mooney (editors), *The Biology of Vines*. Cambridge University Press, Cambridge, United Kingdom.
- Ribeiro, J. E. L. S., M. J. G. Hopkins, A. Vicentini, C. A. Sothers, M. A. S. Costa, J. M. Brito, M. A. D. Souza, L. H. P. Martins, L. G. Lohmann, P. A. C. L. Assunção, E. C. Pereira, C. F. Silva, M. R. Mesquita & L. C. Procópio. 1999. *Flora da Reserva Ducke, Guia de Identificação das Plantas Vasculares de uma Floresta de Terra-Firme na Amazônia Central*. Instituto Nacional de Pesquisas de Amazônia, Manaus.
- Sachs, J. 1882. *Text-book of Botany, Morphological and Physiological*, 2nd ed. Clarendon Press, Oxford, United Kingdom.
- Säll, H. 2002. *Spiral Grain in Norway Spruce*. Växjö University Press, Växjö, Sweden.
- Sands, M. J. S. 2009. The begonias of New Guinea—An overview. *Blumea* 54(1–3): 272–277.
- Scher, J. L., N. M. Holbrook & W. K. Silk. 2001. Temporal and spatial patterns of twining force and lignification in stems of *Ipomoea purpurea*. *Planta* 213: 192–198.
- Schulman, L. & J. Hyvönen. 2003. A cladistic analysis of *Adelobotrys* (Melastomataceae) based on morphology, with notes on generic limits within the tribe Merianieae. *Syst. Bot.* 28(4): 738–756.
- Silk, W. K. & M. Hubbard. 1991. Axial forces and normal distributed loads in twining stems of morning glory. *J. Biomech.* 24: 599–606.
- Silk, W. K. & N. M. Holbrook. 2005. The importance of frictional interactions in maintaining the stability of the twining habit. *Amer. J. Bot.* 92: 1820–1826.
- Thitamadee, S., T. Kazuko & T. Hashimoto. 2002. Microtubule basis for left-handed helical growth in *Arabidopsis*. *Nature* 417: 193–196.
- Welch, C. J. 2002. Chirality in the natural world: Life through the looking glass. Pp. 285–305 in W. J. Lough & I. W. Wainer (editors), *Chirality in Natural and Applied Science*. CRC Press, Boca Raton, Florida.